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BRIEFER ARTICLES.

THE EARLY HISTORY OF ANGIOSPERMS.

THE paper lately published by Mr. HAROLD LYON on the embryo of angiosperms¹ gives a clear account of existing views on the race-history of monocotyledons and dicotyledons. In the course of his argument Mr. LYON has referred to my own work on the subject in very generous terms, while giving in greater detail than before the arguments which had already led him to the opposed conclusion. We are, as before, in complete agreement as to the field of battle. We both hold that monocotyledons and dicotyledons come from a common stock, and that the single cotyledon of the one is strictly homologous with both cotyledons of the other. But on the question of the comparative antiquity of these two classes, we start from opposite ends of the lists. I do not propose to discuss the points on which we differ. The evidence on both sides has been published, and also our respective interpretations. Those interested in the question are in a position to form their own judgment on it. The issue will be determined by the results of future research. But Mr. LYON's lucid statement of the case has shown me that my own is obscure in two points, and I wish to take the first opportunity of restating them.

First I wish definitely to disown the suggestion that the fusion of two ancestral cotyledons might have taken place within the seed where they were acting as sucking organs. This appeared in my first sketch of the whole hypothesis, published in May, 1902.² In later papers³ the fusion of the cotyledons is attributed to the reduction of assimilating organs characteristic of geophilous seedlings in their first season, a second suggestion, inconsistent—as Mr. LYON has pointed out—with the first, which is implicitly abandoned. It would have been clearer to state definitely, as I do here, that—if we consider monocotyledons as derived from a dicotyledous stock by adaptation to a geophilous habit—the fusion of two cotyledons

¹ LYON, HAROLD L., The embryo of the angiosperms. *American Naturalist* **39**:13-25. 1905.

² The origin of the seed-leaf in monocotyledons. *New Phytologist* **1**:107-113. *pls.* 2. 1902.

³ A theory of the origin of monocotyledons. *Ann. Botany* **17**:1-92. *pls.* 1-7. 1903. The evolution of monocotyledons. *BOT. GAZETTE* **37**:325-345. 1904.

into one is simply and sufficiently explained by the necessity of reduction in the green parts of the seedling, and that this explanation of course requires that the ancestral cotyledons should be acting as green assimilating organs above ground during the period of fusion, and excludes my first suggestion that they fused as sucking organs within the seed.

That my argument was obscure in a more important respect I infer from Mr. LYON's statement that the evidence on which it is based could as well be read backwards as forwards; in short that the facts on which I rely might be used to prove the derivation of dicotyledons from monocotyledons. My statement of the argument must have been very defective if it admitted of any doubt on this head. No observer dealing with that evidence at first hand could hold such an opinion. He would find the evidence incomplete; he might rate its value much lower than I do; but so far as it goes he must allow that it points in one direction—the derivation of the single from the double cotyledon. To make this clear, the nature of the evidence must be taken into account. It is of three kinds: anatomical, embryological, general.

The anatomical argument is due to Professors QUÉVA and JEFFREY.⁴ Both have pointed out that the vascular structure of the young stem in monocotyledons is of the exogenous or dictyoledonous type. They both conclude that monocotyledons are derived from dicotyledons. No botanist, I believe, has denied the facts, which I could confirm if necessary. Their theoretical value may be discounted, but the most ingenious critic could hardly use them to prove the descent of dicotyledons from monocotyledons.

The embryological evidence rests primarily on my conclusion that a certain type of vascular structure in the cotyledon and hypocotyl of liliaceous seedlings is primitive, and that various other types of seedling structure in the same family are genetically connected with it. Where we find a single line of related structures there is nothing—in the absence of independent evidence—to show which of the extreme forms is the more primitive. But where—as in this case—there are several distinct lines of descent ending in the same vascular type, it is fair to assume that type as the primitive structure. For a common ancestor naturally gives rise to divergent stocks, but it would be an extraordinary series of coincidences which should lead several distinct types of structure to produce remote descendants of a single type.

It is true that uniform conditions of life do lead to great superficial resemblance between organs which are morphologically distinct. But

⁴ QUÉVA, C., *Contributions à l'anatomie des Monocotylédonées*, p. 147. 1899.
JEFFREY, E. C., in COULTER and CHAMBERLAIN'S *Morphology of Angiosperms*, p. 316. 1903.

the resemblance in such cases is mainly external; the metamorphosis is revealed by differences in internal anatomy. Now in this study of liliaceous seedlings we are dealing with anatomical details which are often uniform, or very nearly so, among allied genera of the most varied external form. Thus, among the Tulipeae some species of *Lilium* have hypogaeic, other species epigaeic cotyledons; the cotyledon of *Fritillaria* is of the common green rush-like form; that of *Tulipa* resembles *Fritillaria*, but the whole structure of the seedling is transformed by the conversion of the stem bud into a dropper. Yet the same vascular symmetry is found in the cotyledon and hypocotyl of all these divergent forms. On the other hand seedlings belonging to almost every tribe of the family possess the green rush-like cotyledon, but it masks a great variety of vascular structure. Thus the reappearance of definite vascular symmetry in several lines of descent cannot in this case be put down to the action of external conditions moulding distinct types to one pattern. The one simple and adequate explanation of the facts is that the various lines of descent started from a common ancestor with vascular symmetry of this persistent pattern.

Now the whole argument from this class of evidence depends on the fact that this vascular type is bisymmetrical. Two equivalent and quite distinct bundles traverse the elongated cotyledon; two traces in the hypocotyl unite to form a tetrarch root. A single type which is symmetrical about two planes is connected with several symmetrical about one. There is no difficulty in supposing all these unisymmetrical types to be descended from the one bisymmetrical type; but it is incredible that the descendants of distinct unisymmetrical types should all become bisymmetrical structures of precisely the same kind. The argument may be neglected, but it cannot be read backwards. It cannot be used to demonstrate the formation of two cotyledons from one.

I do not mean to assert that the evidence quoted cannot be reconciled with the hypothesis of a primitive monocotylous angiosperm. The bilateral cotyledon may conceivably represent a terminal member which becomes modified in one fashion or another into the likeness of a lateral one. But this interpretation of the facts explains only how an apparently lateral member may be descended from a terminal one. It is a study in the derivation of various monocotylous types from a primitive monocotylous form; it gives no clue to the descent of a race with two cotyledons from that form.

The same criticism applies to that class of evidence which I have called general. My reasons for considering monocotyledons as a race specialized from a dicotylous ancestor by adaptation to the geophilous habit have

already been given in this journal. They need not be repeated here. On that hypothesis the formation of one cotyledon from two is due to the necessity of reduction in the aerial organs of seedling geophytes. The tendency to such reduction is shown in other ways. Among dicotyledons the few species which have but one cotyledon are geophilous, so—with one exception—are those which have cotyledons united almost to the top. In many geophilous forms the cotyledons never appear above ground at all, and the first leaf is much reduced in size. Adaptation to a geophilous habit also serves to explain many of the other structural features which are correlated in monocotyledons with the presence of a single cotyledon, notably the stem anatomy.

But though the collective weight of evidence in favor of this view appears to me very great, I have never thought it conclusive. There are no facts to make it incredible that the primitive angiosperm was monocotylous, and that modern dicotyledons derive their two cotyledons from division of the original member. That opinion, however, cannot be deduced from the evidence just given. It is conceivable that the geophilous habit has served simply to specialize monocotyledons, operating to reduce the original terminal cotyledon to an apparently lateral one. But that hypothesis does nothing to explain the rise of dicotyledons from a monocotylous race, and it leaves the very marked similarity in vascular structure between the primitive liliaceous type and certain geophilous species of Ranales out of the question. Yet the approach to a true monocotyledonous structure in some of these forms is most striking, and extends to the mature as well as the seedling plant.

In conclusion, I wish again to point out that my purpose in this communication has been to correct an inconsistency in the former statement of my argument, and further to restate a portion of it which has been misapprehended. I have purposely abstained from criticism of Mr. LYON's alternative hypothesis, and from any attempt to answer his criticisms on mine, except the two which were founded on obscurity in my previous writings.—ETHEL SARGANT, *Quarry Hill, Reigate, England*.